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ORIGINAL ARTICLE

Human impact on vegetation at the Alpine tree-line ecotone during the last millennium: lessons from high temporal and palynological resolution

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Abstract Three mires and a small lake in the Swiss and Austrian Alps were studied palynologically at high resolution, covering the last 1,000, 400, 50 and 1,200 years, respectively. Methodological lessons include: (1) Sub-decadal resolution in upper, little-decomposed peat layers reveals recurrent marked fluctuations in both percentages and influx of regional tree-pollen types, reflecting variations in pollen production rather than in plant-population sizes. (2) Intermittent, single-spectrum pollen maxima in samples of sub-decadal resolution indicate pollen transport in clumps. This type of pollen transport may remain unrecognized in sections with lower sampling resolution, which may then lead to inappropriate interpretation in terms of plant-population sizes. (3) The detection of short-lived phases of human impact in decomposed peat requires sampling intervals as close as 0.2 cm. (4) PAR (pollen influx) may reflect vegetation dynamics more faithfully than percentages. Reliable PAR, however, is difficult to

achieve in Alpine mires due to past human impact on peat growth, even when complex depth–age modelling techniques are used. Critical comparison of PAR with percentages is therefore essential. (5) Careful consideration of spatial scales in pollen signals (local–regional and subdivisions) is essential for a realistic palaeo-ecological interpretation. Results in terms of past human impact on vegetation are summarized as follows: (1) Trends in pollen types reflecting regional human action are in general agreement with earlier findings for the western Swiss Alps, allowing for regional differences. (2) All mires in the Alps investigated here and in an earlier study experienced human impact during the last millennium. The studied small lake, lying in sub-alpine pasture, records forest dynamics at a lower elevation since A.D. 800.

Keywords Alps · Palynology · Last millennium · High resolution · Methods · Human impact

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Introduction

Mires have great potential for the reconstruction of past environments by palaeobotanical methods. The last few centuries to the last millennium have been little studied by these means until recently. One reason for this might be that these periods are considered ‘historical times’, an expression that may give the false impression that ‘everything is basically known’, so that other problems seem much more urgent for palaeoecological research, such as climate change during the Late Glacial and the Holocene and early human activity. However, the response of vegetation to these factors during the last millennium is still incompletely understood. This is regrettable because it is of great interest for the management of natural resources and

the preservation of biodiversity. The study of more recent peat layers and lakes has already yielded unexpected insights. In the western Swiss Alps and Jura Mountains, for example, palynological studies focussing on the vegetation history during the last several centuries showed that all the mires studied, of supposedly immaculate past history, suffered periods of human-related stress, mostly centred around the 19th century in the form of mire grazing (Van der Knaap et al. 2000; Sjögren et al. 2007). Mauntschas mire in the south-eastern Swiss Alps is yet another effort to find a pristine bog that failed, though the details of its failure differ in exciting ways from the earlier efforts (Goslar et al. 2009; Kamenik et al. 2009; Van der Knaap et al. 2011). Another new result was the discovery of pollen trends common to the entire western Swiss Alps (see also Van der Knaap et al. 2001b; Roos-Barracough et al. 2004; Sjögren et al. 2006). The factors that force common pollen trends can be climatic, anthropogenic, or both; in the case of the long-cultivated *Cannabis sativa*, for example, human action was obviously the main driver. In addition, the common pollen trends in the western Swiss Alps and Jura Mountains were found to shift geographically from south to north. The 20th-century *Cannabis* decline can serve as an example; this was more gradual in the south and more abrupt in the north.

This study explores a larger area, including sites in the central and eastern Swiss Alps and the central Austrian Alps, and focuses on human impact on vegetation. The longest and most detailed record is that of Mauntschas in the SE Swiss Alps, which covers the entire last millennium at high temporal resolution, approaching annual for the last 150 years. Van der Knaap et al. (2011) attempted extracting climate signals from Mauntschas using multiple proxies (pollen-based reconstructions of climate and past vegetation, local surface-moisture and surface-pH reconstructions based on testate amoebae, stable carbon and oxygen isotopes in *Sphagnum*, local peat accumulation rates, microscopic charcoal, and macro-fossils). The climate signal, however, appeared to be obscured by the anthropogenic signal. The study included an interpretation of pollen data in terms of strictly local vegetation development and human impact based on a small selection of pollen and spores. Here we extend the interpretation to

wider spatial scales, using all available pollen data. Wengerkopf and Rosaninsee in the central Austrian Alps cover together the last four centuries at high temporal resolution, that for the last 100 years being near annual. Gouillé Rion in the southern Swiss Alps covers the last 1,200 years at an intermediate resolution. The main aim of the paper is to explore a number of aspects of pollen representation that unexpectedly arose from the pursuing of annual temporal resolution and of PAR (pollen accumulation rates or influx) rather than percentages, such as the accuracy of time scales and thus of PAR, pollen transport other than by wind, and spatial scales of the pollen signals.

Description of study sites

Table 1 lists the sites and basic information. Figure 1 shows site locations.

The small lake Gouillé Rion lies in the central Swiss Alps. Tinner et al. (1996) and Tinner and Kaltenrieder (2005) studied the Holocene history of this lake and its surroundings thoroughly using pollen, macrofossils and other proxies. However the last millennium was not dealt with in detail. The site is exposed, high upon the last peak of a ridge. At present, a few scattered *Pinus cembra* trees grow near the site up to 2,350 m elevation, but before ca. 2000 B.C. the site was below the forest limit at 2,400–2,450 m, with *Pinus cembra*, *Larix decidua*, *Betula* and *Alnus viridis* growing close to the lake. Fires and animal husbandry were the cause for the disappearance of the local forest (Colombaroli et al. 2010).

Mauntschas is the largest (ca. 10 ha) mire in the Engadine. The mire is located in more continental conditions in comparison to the western and northern parts of the Swiss Alps. About half of the mire is largely unaffected by human impact and can be considered natural or semi-natural (Grünig 1994). This part of the Swiss Alps, however, has been subject to human activities since the Early Bronze Age; the valley of the study had already become inhabited in about 1950 B.C. (Gobet et al. 2003). The mire is located near the valley bottom (1,600–1,800 m a.s.l.), which extends for ca. 50 km between high (more than 3,000 m a.s.l.) mountain ranges. It is surrounded by forest growing

Table 1 Study sites (see Fig. 1)

| Site name | Country | Latitude | Longitude | Altitude | Size | Type | Collection date |
|--------------|-------------|-----------------|----------------|----------|------------|------|-------------------------------------|
| Gouillé Rion | Switzerland | 46° 09' 25.9" N | 7° 21' 46.5" E | 2,343 m | Ca. 0.5 ha | Lake | 07/1996 |
| Mauntschas | Switzerland | 46° 29' 24.7" N | 9° 51' 16.7" E | 1,818 m | Ca. 10 ha | Mire | 7/08/2003 |
| Wengerkopf | Austria | 47° 10' 36" N | 13° 52' 40" E | 1,780 m | Ca. 0.3 ha | Mire | Top: 12/08/2002 Base: 17/06/2003 |
| Rosaninsee | Austria | 46° 57' 12" N | 13° 46' 50" E | 2,070 m | Ca. 0.3 ha | Mire | 13/08/2002 |

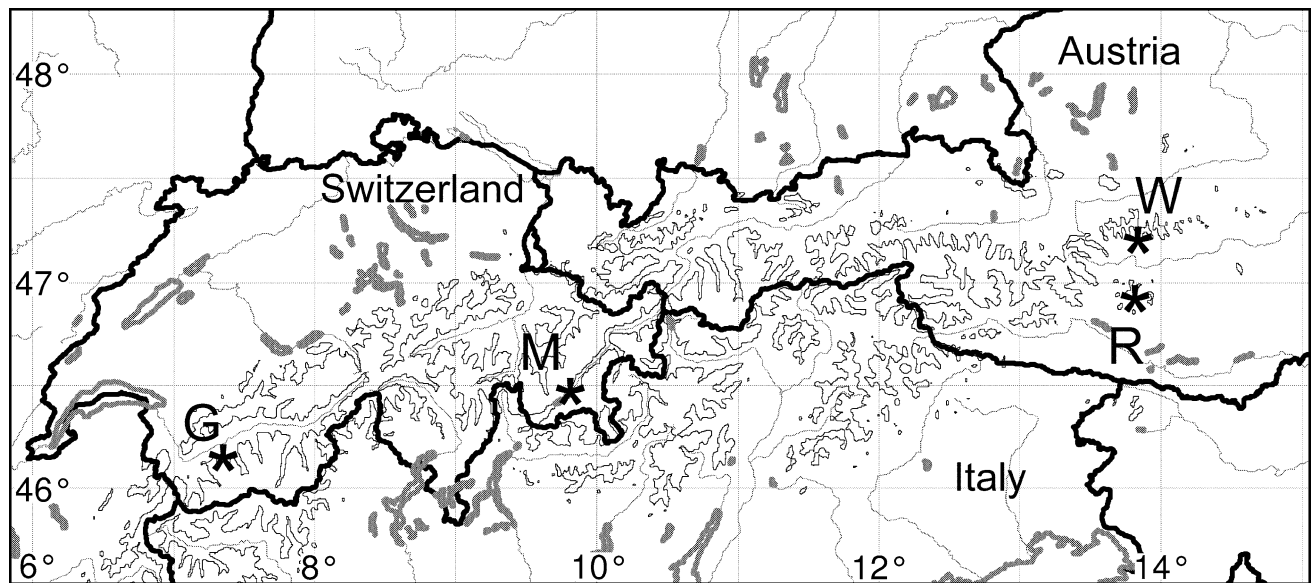


Fig. 1 Study sites (*) are indicated by their initials: Gouillé Rion and Mauntschas in Switzerland; Wengerkopf and Rosaninsee in Austria. Thin grey lines are rivers. Thin black lines show 2,000 m a.s.l. Degrees North and East are indicated. Thick black lines are country boundaries. Thick grey lines are shores.

Thin grey lines are rivers. Thin black lines show 2,000 m a.s.l. Degrees North and East are indicated

to a timberline at ca. 2,100–2,250 m elevation. Close to the mire, the woods are dominated by *Pinus cembra*, which also prevails on the valley bottom and on the lower valley slopes. *Picea abies* is also abundant in the forest close to the mire, and dominates forests in adjacent valleys. With increasing altitude, *Picea* is replaced rapidly, and *Pinus cembra* gradually, by *Larix decidua*, which grows mostly above 1,500 m a.s.l. Pollen of these trees is mainly derived from within the valley, with additional contributions from nearby adjacent valleys (cf. Sjögren et al. 2008a). The forest–mire edge lies about 60 m to the north and west of the collection location, and 200 m south and 500 m east. Erect forms of *Pinus mugo* (ssp. *uncinata*, mountain pine) grow on the mire about 100 m to the southwest. The mire edge has scattered *Salix* shrubs. On the basis of the same peat section used for this study, Kamenik et al. (2009) investigated pollen–climate relationships at Mauntschas during the last 140 years, Lamentowicz et al. (2010) described the hydrological history of the last 140 years on the basis of testate amoebae, and Van der Knaap et al. (2011) used a multi-proxy approach in an effort to separate the climatic from the human signal during the last millennium.

The Wengerkopf mire (Wengerkopfmoos 2 in Krisai et al. 1991; Moor 57053801 in Steiner 1992) sits on top of the mountain of that name, in the Alpine region of Lungau, province of Salzburg, central Austria. The mire is a raised bog of circular form and is ~50 m in diameter. The bog is grazed and surrounded by forest that is also grazed by cattle. The forest has much *Picea abies*, less *Larix decidua* and some *Pinus cembra*. On the bog grow *Pinus mugo* s.s.

krummholz, *Juniperus communis* s.l., stunted *Picea*, *Vaccinium* and *Potentilla erecta*. The peat section studied was taken from a *Sphagnum* hummock, ca. 1.5 m in diameter. The hummock reaches about half a metre above the surrounding peat and consists mostly of well-preserved *Sphagnum capillifolium* and a little *Polytrichum strictum* down to 60 cm from the top, resting on highly decomposed peat. *Sphagnum capillifolium* was identified at four depths (0, 20–25, 40–45 and 55–60 cm). The lithology is described in more detail by Sjögren et al. (2007). Dwarf-shrubs *Juniperus communis* s.l. and *Vaccinium myrtillus* and two small *Picea* trees grow in and through the hummock, which protect the hummock from trampling and support it. Information on the flora of Lungau (in which Wengerkopf and Rosaninsee are situated) comes from Vierhapper (1935), Wittmann et al. (1987), and personal observations.

Rosaninsee is also situated in Lungau, some 25 km south of Wengerkopf. It lies above the actual, but below the potential forest limit. The surroundings are grazed by cattle. The forest-limit ecotone has much *Pinus cembra* and a little *Picea* and an occasional patch of *Pinus mugo*. Some scattered shrubs of *Alnus viridis* occur in the surroundings, but the shrub is not abundant. The mire studied lies at the north-west end of the small lake Rosaninsee. Krisai and Peer (1980) described several mires around this lake, among which is the minerotrophic fen “Rosanin 4” that bears today the sampled ombrotrophic hummock (Moor 471203 in Steiner 1992). Peat thickness of the fen around the hummock is about 10 cm. The hummock consists of *Sphagnum fuscum*, as confirmed at six depths in the sampled section (0–3, 5–10, 10–15, 15–24, 26–30, and 30–32 cm).

Methods

At Gouillé Rion, Willy Tinner collected the studied lake sediment section by the frozen-finger technique (Wright 1980). In Mauntschas mire, a 130 cm long peat monolith was collected with a spade from a *Sphagnum* hummock (diameter ca. 3 m, located in wet peat lawn) in the undisturbed part of the mire. At Wengerkopf, two overlapping peat sections were collected from the *Sphagnum* hummock with a spade: 0–66 cm in 2002 and 58–133 cm in 2003. Exact correlation of the two sections could be made by the transition from well-preserved *Sphagnum* to strongly decomposed peat at 60 cm. At Rosaninsee the peat section was collected with a spade.

Known volumes were sampled for pollen from the sections. The frozen section of Gouillé Rion was sub-sampled by sawing; the sub-samples have a vertical thickness of 1 cm. Further methods follow Tinner et al. (1996). The Wengerkopf section collected in 2002 was sub-sampled in two overlapping sub-sections, 0–28 cm depth and 26–60 cm depth, because of irregularities in the peat stratigraphy. The sub-sections were chosen to avoid the *Juniperus* and *Vaccinium* branches. The sub-sections were cut from the peat with scissors and a sharp kitchen knife while in an unfrozen condition and their dimensions were measured; care was taken not to compress the loose upper peat layers. Sub-sampling for pollen was done unfrozen with scissors at intervals guided by the then available preliminary depth–age model aiming at annual resolution (Goslar et al. 2005); sampling intervals were measured to allow calculation of sample volumes. The peat section of Wengerkopf collected in 2003 was sub-sampled unfrozen with a sharp kitchen knife at 0.2 cm intervals between 60 and 72 cm. Sub-sampling of the Rosaninsee section from the top down to 34.4 cm was done in a way similar to that of the Wengerkopf-2002 sub-sections, aiming at annual resolution, and below 34.4 cm frozen with a sharp kitchen knife. For Mauntschas mire, the peat between 0 and 29 cm was sub-sampled in a way similar to that of the Wengerkopf-2002 sub-sections, whereas below 29 cm it was sub-sampled in a frozen condition in the Institute of Botany and Landscape Ecology (University of Greifswald, Germany) with the ‘Damocles’ device (Joosten and De Klerk 2007).

The pollen samples were cleaned using standard procedures: 6 min of KOH (10%, 90°C), sieving (0.25 mm screen), 2 min acetolysis and 3 min KOH (10%, 60°C). For the determination of pollen concentrations, all samples were taken with known volumes and each sample was spiked with HCl-dissolved *Lycopodium* tablets during the first KOH treatment (Stockmarr 1971). Samples were washed twice with deionised water after sieving and KOH treatment. Cleaned samples were stored in glycerine-water. Pollen was stained with fuchsine for improved contrast.

Pollen and spore percentages were calculated on the basis of a calculation sum including pollen and spores of trees, shrubs, and upland herbs and ferns. Excluded from the calculation sum were wetland taxa like Cyperaceae. Table 2 summarizes numbers of added and counted *Lycopodium* and counted pollen sums. The zonation of the pollen diagrams was guided by the interpretation in terms of human impact on vegetation; for Mauntschas mire it differs in details from the one used in Van der Knaap et al. (2011). Pollen accumulation rates ($\text{grains cm}^{-2} \text{ year}^{-1}$) were calculated on the basis of pollen concentrations and the depth–age models.

Details of the radiocarbon dating of Gouillé Rion and depth–age modelling are given in Tinner et al. (1996). Goslar et al. (2009) developed the final depth–age modelling of the Mauntschas peat section, building on a preliminary modelling in Goslar et al. (2005). It is based on 29 radiocarbon dates and takes into account variations in pollen concentrations. Goslar et al. (2005) also present preliminary depth–age models for Wengerkopf based on 20 radiocarbon dates and for Rosaninsee based on 8 radiocarbon dates; these were further developed here according to the principles used for Mauntschas.

Results and Interpretation

Lithology and dating

The sediment descriptions are listed in Table 3.

The results of depth–age modelling are shown on the pollen diagrams (Figs. 2, 3, 4, 5, and 6). In the Wengerkopf section, the abrupt transitions in lithology at 60 and 63 cm

Table 2 Selected sample statistics: pollen sums and exotics (*Lycopodium*)

| Site | No. of samples | Exotic added: No. tablets \times (No. spores/tablet) | Exotic counted: mean \pm 1 SD | Pollen sum: mean \pm 1 SD |
|--------------|----------------|--|---------------------------------|-----------------------------|
| Gouillé Rion | 37 | $4 \times (12,542 \pm 414)$ | 213 ± 91 | 579 ± 40 |
| Mauntschas | 354 | <48.4 cm: $2 \times (10,679 \pm 192)$ | 770 ± 449 | 314 ± 93 |
| | | >48.4 cm: $2 \times (18,583 \pm 762)$ | | |
| Wengerkopf | 148 | $2 \times (10,679 \pm 192)$ | 926 ± 735 | 653 ± 102 |
| Rosaninsee | 48 | $2 \times (10,679 \pm 192)$ | 455 ± 317 | 733 ± 67 |

Table 3 Lithology

| Base cm | Description | Lower boundary |
|--|--|----------------|
| Gouillé Rion | | |
| 3.0 | Gyttja | Gradual |
| 8.5 | Silvery-white silt | Gradual |
| 36 | Slightly silty gyttja | Gradual |
| 43 | Silty gyttja | Gradual |
| 52 | Slightly silty gyttja | |
| Mauntschas mire ^a | | |
| 5.0 | Well-preserved erect <i>Sphagnum fuscum</i> | Gradual |
| 9.3 | Well-preserved, randomly lying <i>Sphagnum fuscum</i> | Rather abrupt |
| 16.5 | Well-reserved, randomly lying <i>Sphagnum</i> + abundant vascular plants | Rather abrupt |
| 17.0 | Oblique layer of horizontally lying mosses | Rather abrupt |
| 35.5 | Rather well preserved, randomly lying <i>Sphagnum</i> | Gradual |
| 58.0 | Somewhat decomposed, randomly lying <i>Sphagnum</i> + vascular plants | Gradual |
| 72.0 | Rather decomposed, randomly lying <i>Sphagnum</i> + vascular plants | Rather abrupt |
| 75.5 | Rather decomposed peat + abundant vascular plants | Gradual |
| 80.0 | Decomposed peat + abundant vascular plants | Gradual |
| 83.0 | Decomposed peat + some vascular plants | Gradual |
| 87.5 | Decomposed peat + few vascular plants | Gradual |
| 91.0 | Decomposed peat + some vascular plants | Gradual |
| 99.0 | Rather decomposed <i>Sphagnum</i> peat + vascular plants | Gradual |
| 104.5 | Decomposed fibrous peat | |
| Wengerkopf: Peat section collected in 2002 | | |
| 2.0 | Green, very well preserved, erect <i>Sphagnum</i> | Gradual |
| 5.0 | Light green-yellow, very well preserved, erect <i>Sphagnum</i> | Gradual |
| 13.0 | Light brown–red, very well preserved, erect <i>Sphagnum</i> | Gradual |
| 14.0 | Light brown–red, very well preserved, randomly lying <i>Sphagnum</i> | Gradual |
| 22.5 | Light brown–red, very well preserved, partly erect <i>Sphagnum</i> | Gradual |
| 33.0 | Red-brown, well preserved, partly erect <i>Sphagnum</i> + many roots | Gradual |
| 49.0 | Yellow–brown, well-preserved, randomly lying <i>Sphagnum</i> | Gradual |
| 54.0 | Brown, well-preserved, randomly lying <i>Sphagnum</i> | Gradual |
| 58.0 | Grey-brown, well-preserved, randomly lying <i>Sphagnum</i> | Gradual |
| 60.0 | Grey-brown, moderately preserved, randomly lying <i>Sphagnum</i> | Abrupt |
| Wengerkopf: Peat section collected in 2003 (> 58 cm) | | |
| 60.0 | Grey-brown, moderately preserved, randomly lying <i>Sphagnum</i> | Abrupt |
| 63.0 | Dark brown, decomposed <i>Sphagnum</i> peat | Rather abrupt |
| 65 | Brown-black, very strongly decomposed peat | Gradual |
| 75 | Dark brown, strongly decomposed peat | Gradual |
| Rosaninsee | | |
| 1.0 | Green, very well preserved, erect <i>Sphagnum</i> | Gradual |
| 12.0 | Light red-brown, very well preserved, erect <i>Sphagnum</i> | Gradual |
| 13.5 | Light red-brown, very well preserved, erect <i>Sphagnum</i> + <i>Polytrichum</i> | Gradual |
| 22.0 | Light red-brown, very well preserved, erect <i>Sphagnum</i> | Gradual |
| 27.5 | Red-brown, well preserved, randomly lying <i>Sphagnum</i> | Gradual |
| 31.0 | Brown, rather well preserved, randomly lying <i>Sphagnum</i> | Abrupt |
| 34.0 | Dark red-brown, loose, rather decomposed <i>Sphagnum</i> + roots | Abrupt |
| 36.5 | Black, compact, decomposed peat + roots | Rather abrupt |
| 44.0 | Brown, compact, strongly decomposed peat | Gradual |
| 52.0 | Grey-brown, compact, strongly decomposed peat + some sand | Gradual |
| 55.0 | Brown-grey, compact, sandy peat | End of section |

^a Vascular plant remains are mainly cf. Cyperaceae fibres

are an indication that the net accumulation of peat may have been interrupted (Sjögren et al. 2007). However this could not be taken into account in the depth–age modelling, so the modelled ages below 60 cm depth have an error of unknown size.

At Mauntschas, the periods A.D. 1130–1230 (92.0–91.6 cm) and A.D. 1655–1700 (78.8–78.6 cm) differ from adjacent periods in having very low peat accumulation, and, anticipating the pollen results, also low pollen accumulation rates (Fig. 3). The low pollen accumulation rates extend up to A.D. 1745 (77.6 cm) for the later period. Pollen percentages, however, do not show trends different from directly adjacent periods (Fig. 4). Two explanations seem possible: (1) Plants had generally low pollen productivity in these periods, possibly for climatic reasons; or (2) the observed minima in pollen accumulations are an artefact of the depth–age model, whereas the percentages convey a more realistic situation. The first explanation is unlikely, because it would imply that the supposed adverse weather conditions would have the same impact on plants with widely different ecologies and positions in the field (especially elevation). The second explanation would imply that the two sediment sections include a hiatus (missing peat = missing time record). Experiments with depth–age modelling (not shown here) support this possibility; the introduction of a hiatus of about four decades (30–50 years) in both sediment sections removes the minima in calculated pollen accumulation. The calibrated radiocarbon dates do not provide any hints for or against the hiatus hypothesis. In the final depth–age modelling of the peat section (Goslar et al. 2009) this possibility was not explored in order to keep the complexity of the model within limits. We are nevertheless inclined to accept the hiatus hypothesis as the most likely. We therefore base for these periods the interpretation of the pollen results on percentages rather than on accumulation rates.

The pollen results are presented as percentage pollen diagrams in Fig. 2 (Gouillé Rion), Figs. 3, 4 (Mauntschas; also PAR), Fig. 5 (Wengerkopf) and Fig. 6 (Rosaninsee). The pollen diagrams show a selection of more frequent pollen types, omitting the numerous rare ones that do not show stratigraphic differentiation.

Gouillé Rion

Much of the pollen in Gouillé Rion (Fig. 2) reflects a large region due to the high elevation of the site (2,343 m a.s.l.) and the open, exposed situation, where virtually no trees grow today apart from a few stunted *Larix* (<1 m tall). Tree *Betula* is sparsely present near the site today, but was abundant there during zone GR4-2.

Zone GR4-1 is roughly dated to A.D. 800–980. Pollen suggests that *Alnus viridis* was more abundant than the few

scattered shrubs that are still present today. The increased *Rumex acetosa*-type pollen supports this, representing *Rumex alpestris* that is mostly abundant around *Alnus viridis*, profiting from soil nitrogen produced by this shrub. *Secale*, *Cerealia* and *Cannabis* indicate abundant agriculture in the lowlands, *Plantago lanceolata* grasslands at lower elevation, and *Artemisia* nutrient-poor vegetation on skeletal soils at much lower elevation.

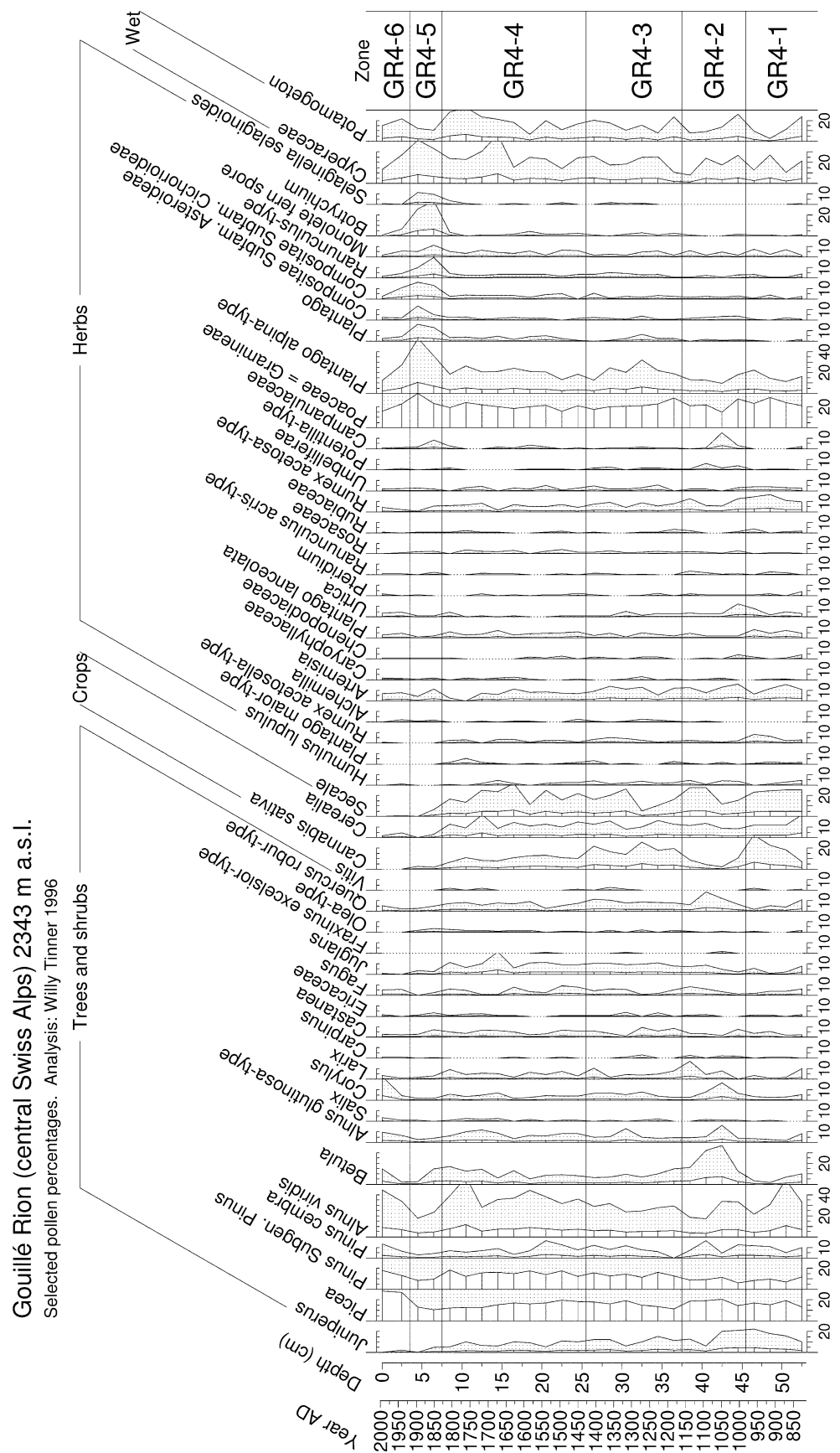
Zone GR4-2 is roughly dated to A.D. 980–1150. A marked minimum in *Cannabis* pollen indicates a decline in its cultivation, whereas *Secale* and *Cerealia* do not show any minimum. Pollen maxima indicate temporary tree recovery at all elevations: *Betula* and *Larix* at high and middle elevations, *Picea*, *Abies* and *Alnus glutinosa*-type at middle elevation, and *Corylus* and *Quercus* at low elevations. *Juglans*, cultivated at low elevation, increased gradually around A.D. 1100. Maxima of Campanulaceae and *Potentilla*-type indicate local vegetation change, but probably not a decrease in grazing pressure for which there are no indications. Also the *Urtica* maximum is possibly local, though regional pollen distribution can not be excluded (Jochimsen 1986). The pollen maxima of different types in this zone do not coincide exactly, but the temporal resolution of the diagram is insufficiently high to draw any conclusions from this.

Zone GR4-3 is roughly dated to A.D. 1150–1480. Pollen indicates a vegetation much like that in zone GR4-1, but differs in the increased presence of *Castanea*, *Juglans* and *Pinus sylvestris* at lower elevation and by increased local grazing pressure indicated by decreased *Juniperus* (*communis* s.l.) and gradually increasing *Plantago alpina*.

Zone GR4-4 is roughly dated to A.D. 1480–1825. The pollen diagram indicates no more than a modest change in vegetation. *Cannabis* cultivation decreased, and the abundance of *Alnus viridis* increased slightly. No change in local grazing pressure is recorded nor any change in tree abundance at any elevation.

Zone GR4-5 is very roughly dated to A.D. 1825–1950. The layer of silvery-white silt indicates erosion in the catchment, where this material still today lies exposed on the surface within a few metres of the lake. The maxima of *Botrychium* and *Selaginella selaginoides* spores and Compositae and *Plantago* pollen must be related to the erosion, most likely representing surface-water transport together with the silt. The average tree-pollen concentrations (not shown) are about half of those of the underlying layers, which suggests higher sediment deposition rates rather than a single erosion event. The largest Holocene glacier advance in the Swiss Alps is dated close to A.D. 1850, fitting nicely to the rough age estimate and the radiocarbon date from the silt layer in the parallel core studied by Tinner et al. (1996), who argued that the erosion was related to the harsh climatic conditions of the Little Ice

Fig. 2 Pollen diagram for Gouillé Rion at the tree limit in the central Swiss Alps. Values are pollen percentages based on the sum of pollen and spores of dry-ground vascular plants; percentages of other pollen and spores are based on the same sum. Percentages are drawn as curves with depth bars at sample midpoints; the grey scale is exaggerated 5×. Selected pollen types are shown





Age. Van der Knaap et al. (2000), on the other hand, reconstructed maximum grazing pressure during the 19th century in many middle to high-alpine sites in the Swiss

Alps. Both the severe climatic conditions and the increased grazing pressure may have contributed to the increased erosion.

Zone GR4-6 is roughly dated to A.D. 1950–1996. In agreement with the general trend in western Switzerland (Van der Knaap et al. 2000), we see an increase in *Picea* and a decline in the annual crops (*Secale*, *Cereal*ia and *Cannabis*).

Mauntschas

Principles of interpretation

Table 4 provides a grouping of palynomorphs in Mauntschas based on similarities in trends, with a rough assessment for each group of the ecological significance and the spatial scale of interpretation. The ecological assessment takes the local situation into account, such as the proximity of the forest limit to the site, the forest composition in the surroundings, and vegetation patterns in relation to human activity. Also the assessment of spatial scales takes into account the local situation, in addition to general knowledge of pollen productivity generated in the Swiss Alps and surroundings (Mazier et al. 2008; Soepboer et al. 2007; Van der Knaap et al. 2001a, 2010; Sjögren et al. 2008a, b; Sjögren et al. 2010). The pollen diagrams (Figs. 3, 4) follow this grouping.

Spatial scales of the reconstructed events are extremely important for ecological understanding, so they were considered carefully. If pollen of a taxon with low pollen productivity is found at all, the pollen trends (increases or decreases) reflect events on a local scale (of the order of metres: at or close to the study site). *Primula farinosa* (group 4) is a good example. At the other extreme, pollen with very high productivity like *Olea* and pollen of other plants known not to occur within tens of km of the site are assigned to the extra-regional scale (group 8). Between these extremes is the extra-local scale (tens of metres), mostly corresponding to moderately low pollen productivity, and the regional scale (hundreds of metres to a few km), mostly corresponding to moderately high pollen productivity. The actual distance of plant populations to the study site, however, modifies the scale. These distances are known for the top of the core (modern), and the distances for down-core can be guessed from the pollen trends: spikier curves indicate closer proximity of the pollen source. For example, *Picea* pollen spreads well, which would suggest an extra-regional scale, but the dense *Picea* tree stands close to the site contribute so much pollen that the pollen trends are regional.

Plant abundance and proximity is inferred as dominating the pollen trends of the trees that make up group 1, so the scale is regional. Van der Knaap et al. (2011) concluded that climate does not significantly influence their pollen productivity. Most herbs and the fungi (groups 2–7) have low pollen/spore-dispersal capacities, so the scale is local.

Among them, Gramineae and *Plantago* species (group 4) have somewhat better pollen-dispersal capacities, but the scale is still local to extra-local since their higher pollen maxima indicate that the plants grew at a close distance. The same is valid for *Calluna*, *Juniperus* (group 5), and Cyperaceae (group 6). *Pinus* Subgen. *Pinus* pollen (group 6) represents mainly *Pinus mugo* ssp. *uncinata* growing on mire, also on Mauntschas today, so the scale is extra-local. Long-distance transported pollen (group 8) is extra-regional. S.C.P. (spheroidal carbonaceous particles or industrial soot) is also of distant origin.

Reconstruction of mire-surface wetness from pollen data is not without problems, because local human impact confuses the signal and because of taxonomic imprecision. For example, Cyperaceae pollen may derive from *Eriophorum vaginatum* on desiccated bog, from *Eriophorum angustifolium* and *Carex rostrata* in wet fen, or *Trichophorum cespitosum* on wet or dry grazed mire, all of which occur in Mauntschas today. Some members of group 4 are good wetness indicators (*Ranunculus aconitifolius*-type, *Trollius*, *Caltha*-type, and *Scutellaria*-type), whereas others also grow in dry meadows or pastures. Macrofossil information appeared to be helpful, whereas the testate amoebae studied in the same peat section provided the most solid basis for estimating surface wetness (Van der Knaap et al. 2011).

Local to regional past vegetation, environment, and human impact

Table 5 provides a short summary of reconstructed human impact on the mire and its surroundings.

Zone MA-P1a High *Picea* values indicate a low disturbance level close to the mire. Low values of *Plantago alpina*, *Ranunculus acris*-type (group 4) and *Potentilla*-type (group 5) suggest anthropogenic grasslands (pastures, hay meadows) away from the mire.

Zone MA-P1b *Picea* and *Larix* pollen accumulations remain approximately constant, whereas percentages decline. This suggests a percentage effect, mostly due to increasing pollen accumulation of *Pinus* Subgen. *Pinus*. The latter indicates an expansion of *Pinus mugo* s.l. on the mire.

Zone MA-P1c The decline of *Pinus* Subgen. *Pinus* (group 6) can hardly be explained by felling, because *Pinus mugo* or *Pinus sylvestris* would not be of any interest to humans when there was so much *Pinus cembra* and *Larix* around. A wetter mire surface may have caused *Pinus mugo* to decline and Cyperaceae (group 6) to expand. Testate amoebae, however, do not indicate a change in surface

Mauntschas: Pollen percentages

Pollen types showing vegetation dynamics
Types followed by () are not in pollen sum. Note scale differences

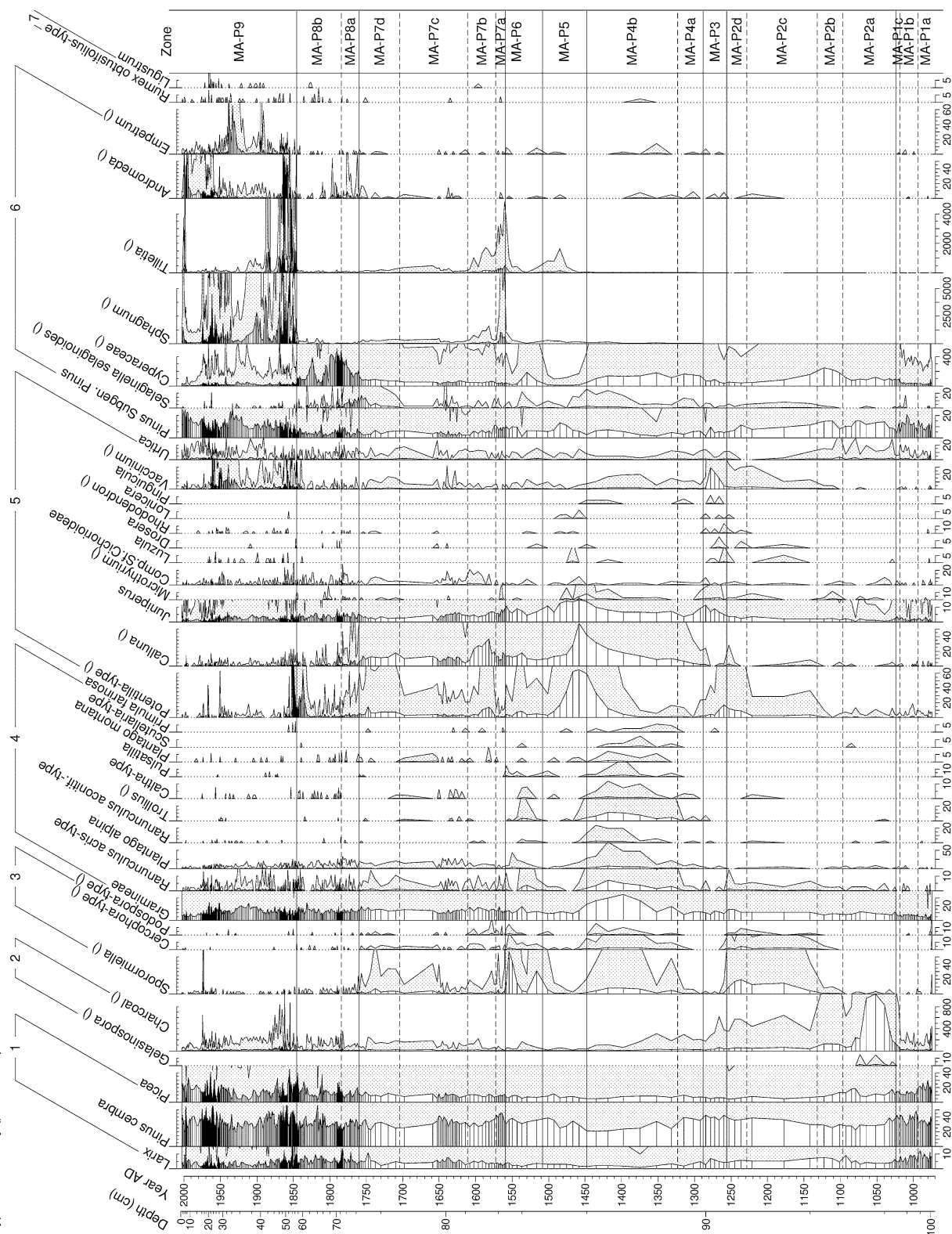


Fig. 4 Pollen diagram for Mauntschas mire in the upper conifer belt of the south-eastern Swiss Alps. Values are pollen percentages based on the sum of pollen and spores of dry-ground vascular plants; percentages of other pollen, spores, and palynomorphs are based on

the same sum. Percentages are drawn as *curves with depth bars* at sample midpoints; the *grey scale* is exaggerated 10×. Pollen types and groups are as in Fig. 3 and Table 4; pollen groups 8 and 9 are shown in Fig. 4

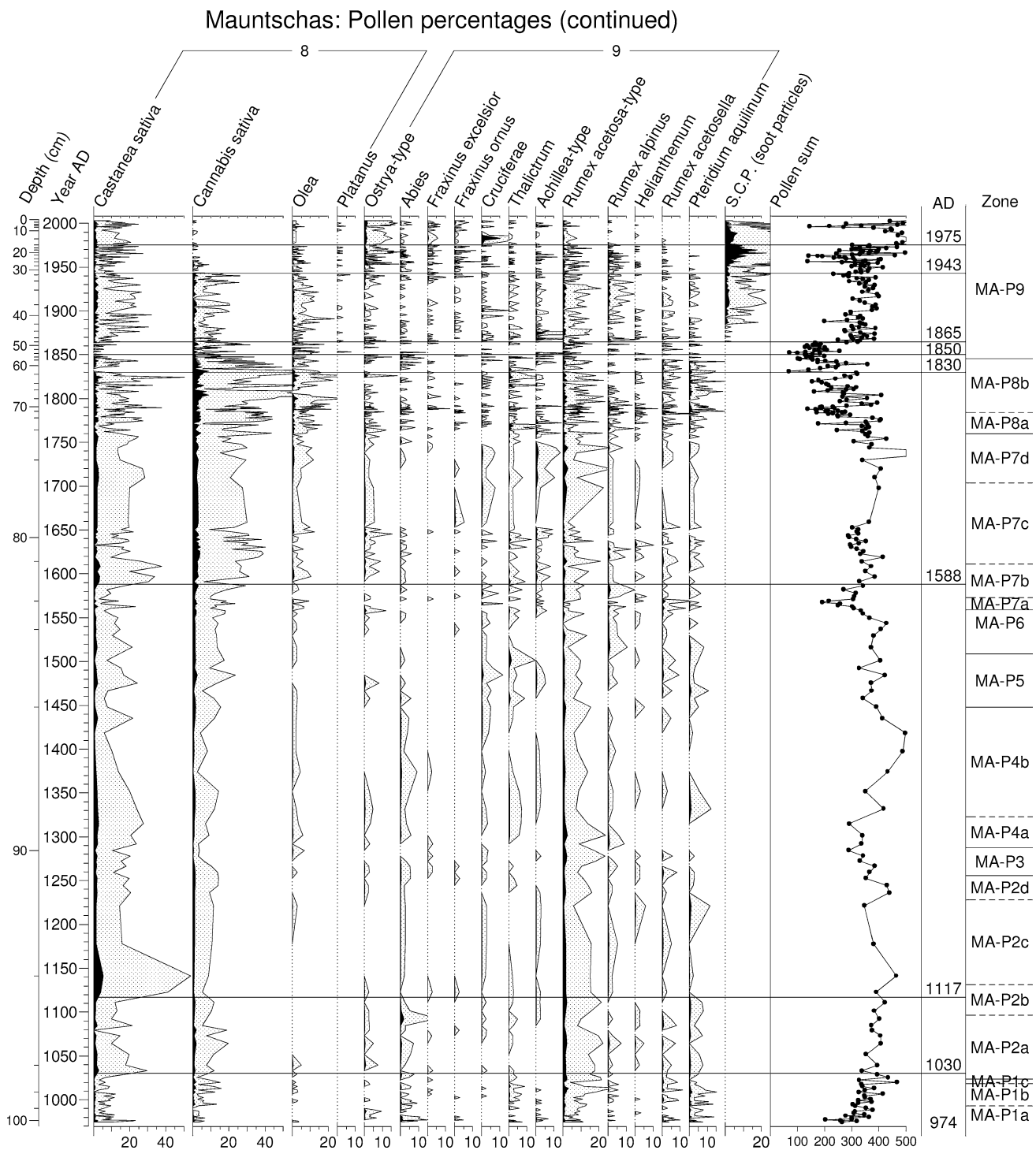


Fig. 4 continued

wetness (Van der Knaap et al. 2011), but this may be a matter of spatial scale; testate amoebae are strictly local, whereas the pollen reflects a larger surface.

Zone MA-P2a *Gelasinospora* and charcoal (group 2) indicate burning. This may be related to the moderate

decrease of *Larix* and *Pinus cembra*, possibly through direct human impact on the surrounding forest. Other indications of human impact by way of grazing on the mire are the renewed appearance of *Sporormiella* (group 3), the drier local conditions as reconstructed through testate amoebae, and the decreased peat accumulation rate.

Wengerkopf (Lungau, Austria) 1790 m a.s.l.

Pollen percentages (selected types)
Analysis: Jacqueline van Leeuwen
Note scale differences

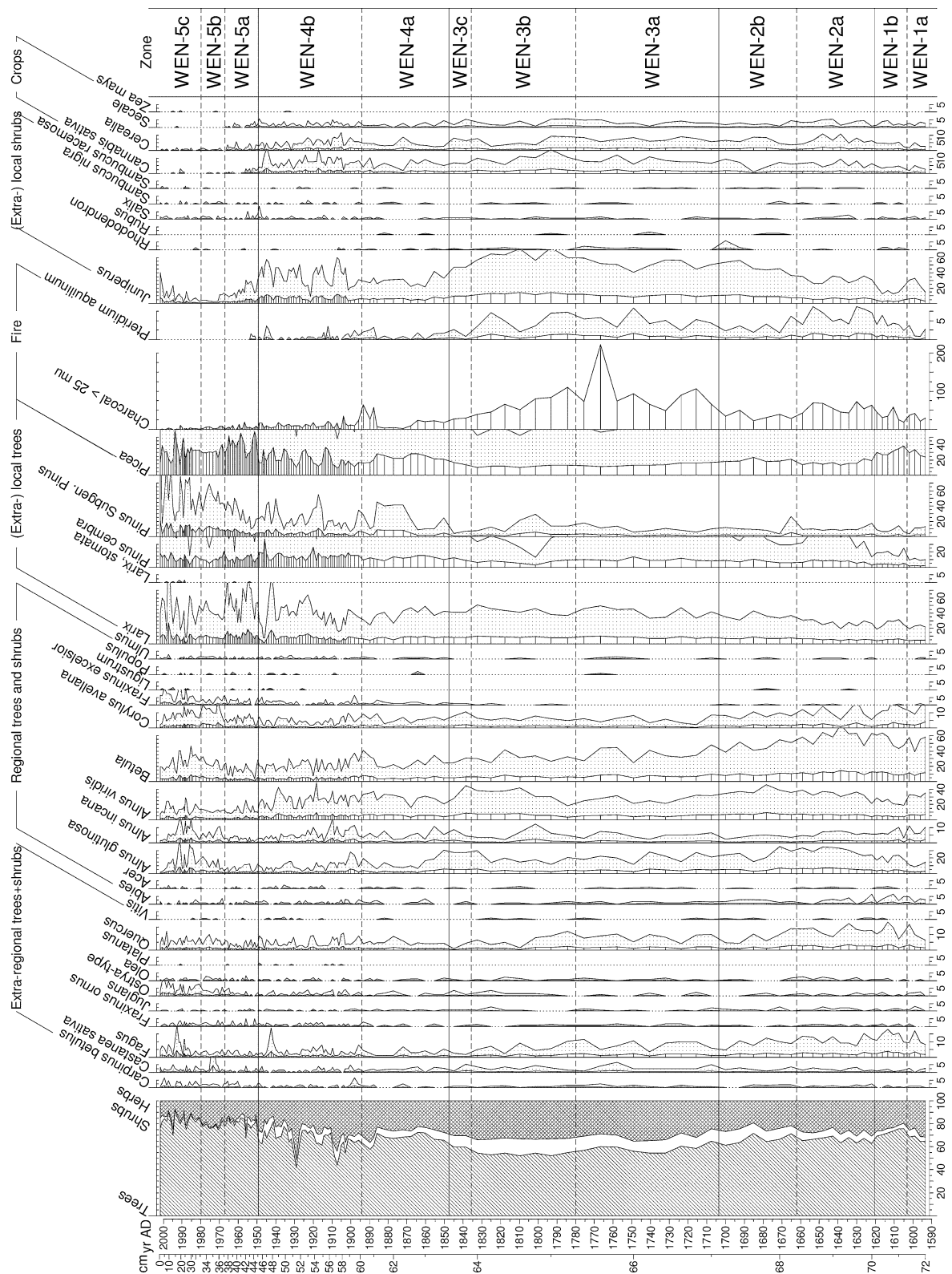


Fig. 5 Pollen diagram for Wengerkopf mire (Lungau region) in the upper conifer belt of the central Austrian Alps. Values are pollen percentages based on the sum of pollen and spores of dry-ground vascular plants; percentages of other pollen, spores, and

palynomorphs are based on the same sum. Percentages are drawn as curves with depth bars at sample midpoints; the grey scale is exaggerated 5×. Selected pollen types are shown. The group of Herbs 1 is discussed in the text

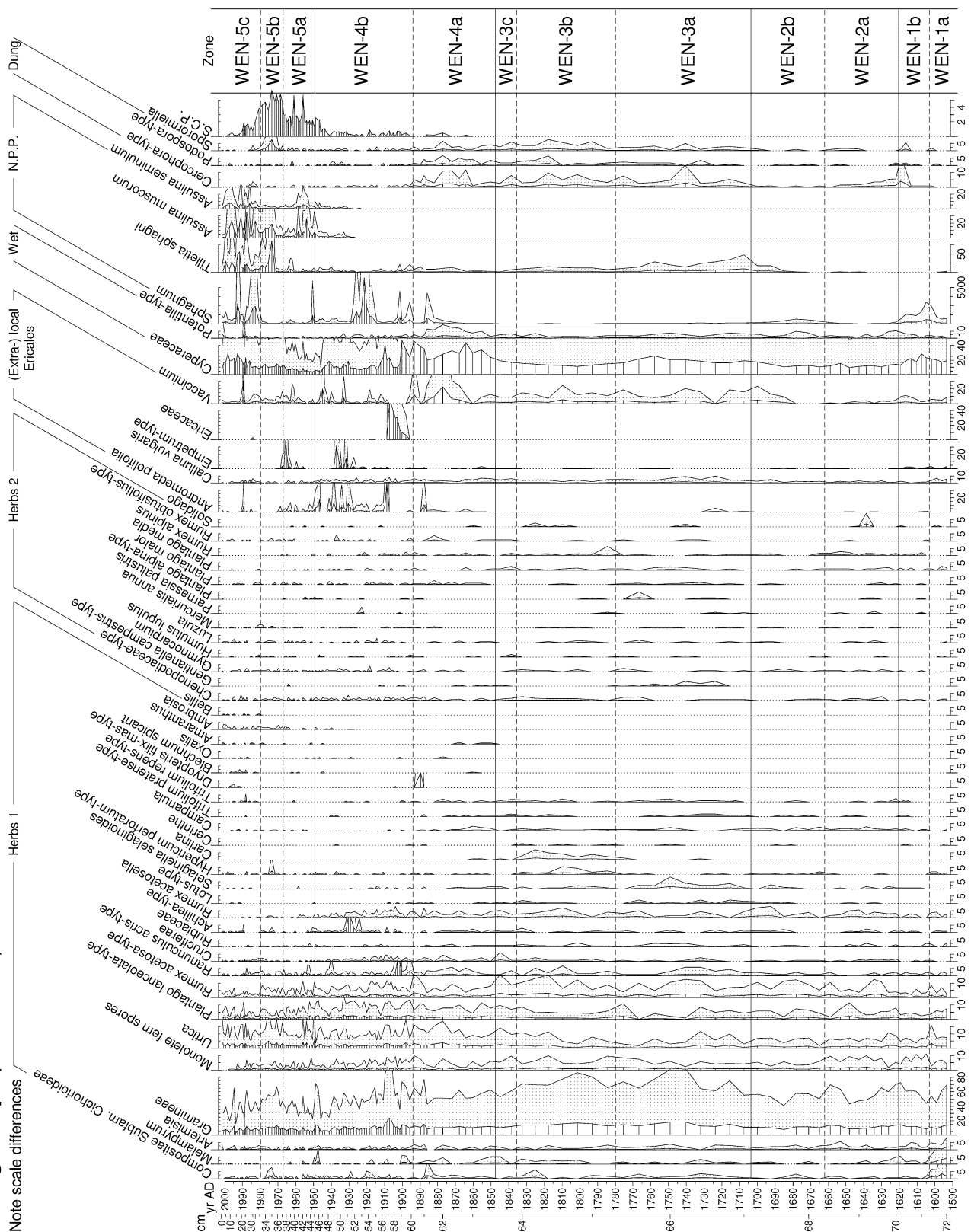


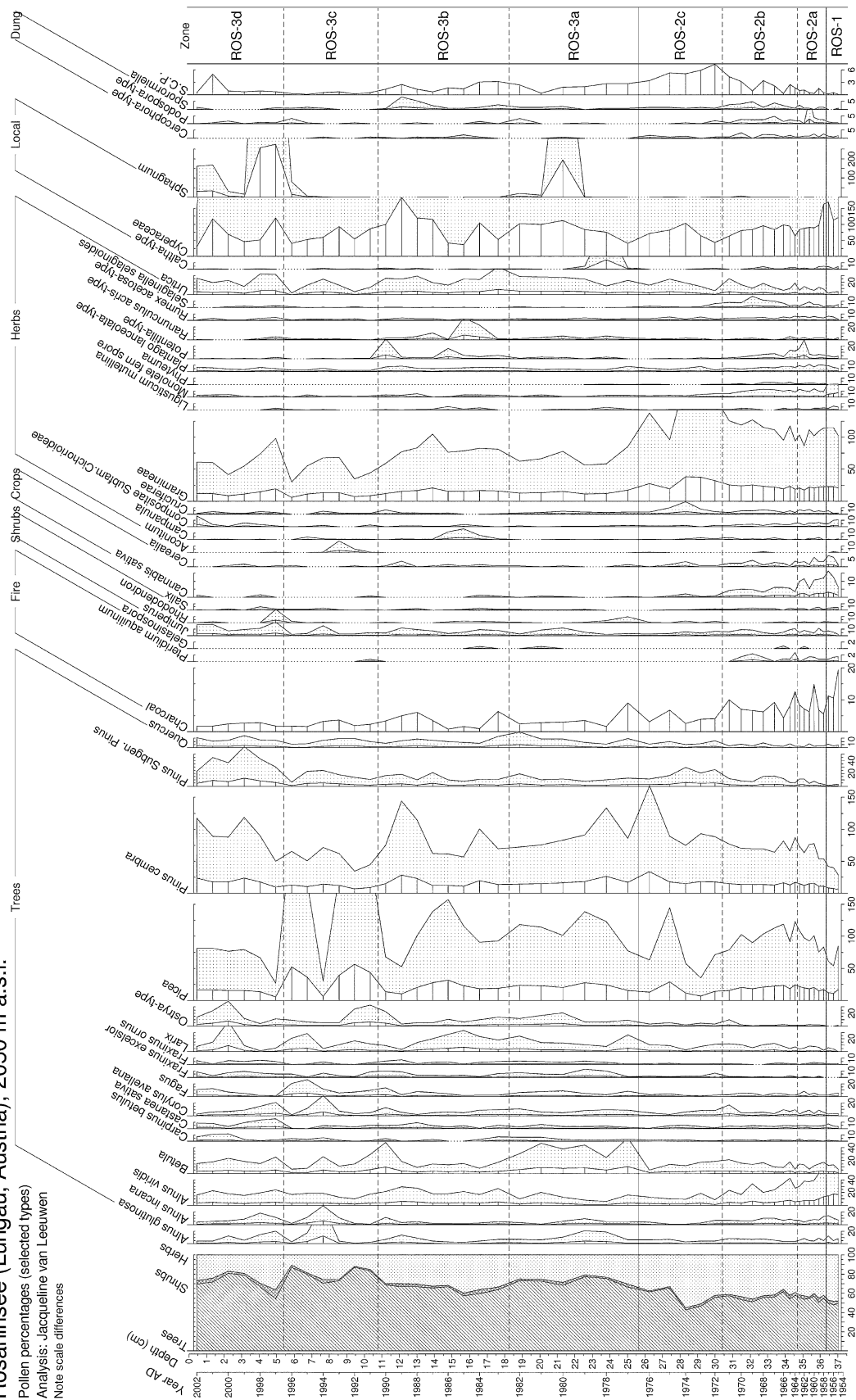
Fig. 5 continued

Rosaninsee (Lungau, Austria), 2050 m a.s.l.

Pollen percentages (selected types)

Analysis: Jacqueline van Leeuwen

Note scale differences



◀ **Fig. 6** Pollen diagram of Rosaninsee at the tree limit in the central Austrian Alps. Values are pollen percentages based on the sum of pollen and spores of dry-ground vascular plants; percentages of other pollen, spores, and palynomorphs are based on the same sum. Percentages are drawn as *curves with depth bars* at sample midpoints; the *grey scale* is exaggerated 5×. Selected pollen types are shown

Zone MA-P2b The increase of dung-related fungal spores (group 3) and the maximum of Cyperaceae indicate more grazing on the mire.

Zone MA-P2c In view of a possible hiatus (see above), we ignore the minima present in accumulation rates (Fig. 3) but absent in percentages (Fig. 4) (group 1: charcoal, Gramineae and *Pinus* Subgen. *Pinus*). The decline of *Picea* together with the expansion of nutrient-poor grassy heathland (groups 4–6: *Vaccinium*, *Potentilla*-type, *Selaginella selaginoides*, *Ranunculus acris*-type; presence of *Juniperus* and *Calluna*) suggests the removal of trees by humans from the marginal zone of the mire. The increase of dung-related fungal spores (group 3) suggests increased grazing, but there is no indication of nutrient enrichment of the vegetation. The minimum of *Urtica* suggests rather a nutrient depletion. This suggests that the humans extracted nutrients from the area, and possibly collected *Urtica* and took it away as animal fodder or human food.

Zone MA-P2d The maxima of dung-related fungal spores (group 3) indicate grazing on the mire. The increase in

Gramineae, *Vaccinium* and *Potentilla*-type also point to human impact on the mire.

Zone MA-P3 The decline of dung-related fungal spores indicates cessation of grazing on the bog. Another indication of reduced grazing is the decline of Gramineae and the maxima reached by heathland shrubs (group 5: *Juniperus*, *Vaccinium*, *Rhododendron*, *Lonicera* and appearance of *Empetrum*), *Luzula* and *Microthyrium*, which suggests that heathland taxa could invade the grassland close to the bog or on the dry bog margin when the grazing pressure diminished. The calcareous-fen taxa *Primula farinosa* and *Pinguicula* appeared.

Zone MA-P4a This zone is transitional to the next zone in some respects. The peat accumulation rate declined further, Cyperaceae increased abruptly and *Calluna* slowly, which together are indicative of a dry mire surface. Testate amoebae, on the other hand, indicate very wet conditions especially during this period (Van der Knaap et al. 2011); the exact sampling location may have been a hollow whereas the pollen and spores reflect nearby hummocks. The heathland shrubs (other than *Calluna*) declined, some grassland taxa started a modest increase (*Plantago alpina*, *Trollius europaeus* and *Selaginella selaginoides*), and dung-related fungi remained virtually absent. This suggests that the dry nutrient-poor heathland postulated for the bog margins was transformed to equally dry, nutrient-rich herb vegetation in the absence of grazing animals. This

Table 4 Pollen groups in Mauntschas (Figs. 3, 4)

| Group ^a | Taxa ^b | Indicative of | Spatial scale |
|--------------------|--|---|----------------------|
| 1 | <i>Larix</i> , <i>Pinus cembra</i> , <i>Picea</i> | Forest | Regional |
| 2 | <i>Gelasinospora</i> ; Charcoal | Burning | Local |
| 3 | Dung-related fungal spores: <i>Sporormiella</i> , <i>Cercophora</i> -type, <i>Podospora</i> -type | Grazing animals | Local |
| 4 | Gramineae, <i>Ranunculus acris</i> -type, <i>Plantago alpina</i> , <i>Ranunculus aconitifolius</i> -type, <i>Trollius</i> , <i>Caltha</i> -type, <i>Pulsatilla</i> , <i>Plantago montana</i> , <i>Scutellaria</i> -type, <i>Primula farinosa</i> | Wet meadow or pasture | Local to extra-local |
| 5 | <i>Potentilla</i> -type, <i>Calluna</i> , <i>Juniperus</i> , <i>Microthyrium</i> , Compositae Subfam. Cichorioideae, <i>Luzula</i> , <i>Drosera</i> , <i>Rhododendron</i> , <i>Lonicera</i> , <i>Pinguicula</i> , <i>Vaccinium</i> , <i>Urtica</i> | Pasture on dry heathland or on degraded bog | Local to extra-local |
| 6 | <i>Pinus</i> Subgen. <i>Pinus</i> , <i>Selaginella selaginoides</i> , Cyperaceae, <i>Sphagnum</i> , <i>Tilletia</i> , <i>Andromeda</i> , <i>Empetrum</i> | Mire and bog | Local to extra-local |
| 7 | <i>Rumex obtusifolius</i> -type, <i>Ligustrum</i> | Nutrients/Planted | Regional |
| 8 | <i>Castanea</i> , <i>Cannabis</i> , <i>Olea</i> , <i>Platanus</i> | Cultivation | Extra-regional |
| 9 | <i>Ostrya</i> -type, <i>Abies</i> , <i>Fraxinus excelsior</i> , <i>Fraxinus ornus</i> , Cruciferae, <i>Thalictrum</i> , <i>Achillea</i> -type, <i>Rumex acetosa</i> -type, <i>Rumex alpinus</i> , <i>Helianthemum</i> , <i>Rumex acetosella</i> , <i>Pteridium</i> | [See text] | Not local |

^a Groups 1–9 are shown in Figs. 3 and 4

^b *Group 1* Dominant forest trees near the study site within several km. *Group 4* Gramineae, *Ranunculus acris*-type and *Plantago alpina* are also abundant in dry meadow/pasture. *Group 6* Today *Pinus* Subgen. *Pinus* (inc. *Pinus mugo* ssp. *uncinata*) grows on the dry bog parts of Mauntschas; *Selaginella selaginoides* is also frequent in pasture, and Cyperaceae in any moist grassland. *Group 8* Ecologically heterogeneous, responding to changing cultivation practices. *Group 9* Ecologically heterogeneous: trees from outside study valley, herbs not growing locally

points to the creation of hay meadows in the marginal zone of the mire.

Zone MA-P4b Testate amoebae indicate that the exact sampling location became drier (Van der Knaap et al. 2011), the maximum of dung-related fungal spores (group 3) and *Selaginella selaginoides* indicate local grazing, and peat accumulation rates reached a minimum. The trampling that is always associated with grazing probably caused drying of the surface and compaction of the peat (Sjögren et al. 2007). In contrast with this, a wide range of pollen types shows that nutrient-rich, periodically flooded grassland was quite close and therefore on the mire, at the order of a few metres away judging by the poor dispersal properties of several of the taxa (group 4: *Trollius europaeus*, *Caltha palustris*, *Pulsatilla alpina*, *Scutellaria galericulata*, *Primula farinosa*). A possible scenario is that the cattle were kept overnight at a summer farm close to the mire, and the manure collected was used to enrich the water flow directed to irrigate the edges of the mire with the aim of increasing fodder or hay

production. Grassland irrigation is common practice in mountain areas that have a precipitation deficit in summer (personal observations). The ruin of a building at the mire edge <100 m from the sampling site, of unknown age but more recent than the period discussed here, supports this possibility. *Larix* (group 1) has a minimum, which suggests that the tree was removed for use.

Zone MA-P5 A decline in both grazing and manuring is indicated by increased peat accumulation, a marked decline in dung-related fungal spores, and the virtual disappearance of indicators of nutrient-rich wet grassland. The local grassland became overgrown by less nutrient-demanding heathland, as indicated by the maxima of *Juniperus*, *Calluna* and *Potentilla*-type and the minimum of Gramineae. An additional sign of nutrient-poor conditions is the expansion to dominance of *Sphagnum fuscum* (Van der Knaap et al. 2011), a lawn or hummock-forming species of ombrotrophic conditions. Together, this indicates a strong reduction in human activity on and near the mire, to a level similar to Zone MA-4a.

Table 5 Summary of (extra-) local human impact on Mauntschas mire

| Zone | Bottom (cm) | Bottom (age) | Type and scale of human impact on mire (local) and surroundings (regional) | Strength of human impact on mire (local) |
|--------|-------------|--------------|--|--|
| MA-P9 | 57.35 cm | A.D. 1845 | Mire vegetation patterns change, probably unrelated to human action | Weak or absent |
| MA-P8b | 72.5 cm | A.D. 1784 | Mire vegetation patterns change, probably unrelated to human action | Weak or absent |
| MA-P8a | 76.5 cm | A.D. 1760 | Less grazing; further vegetation shifts | Weak or absent |
| MA-P7d | 78.5 cm | A.D. 1704 | Grazing on mire declined; mire vegetation patterns changed, probably unrelated to human action | Weak |
| MA-P7c | 82.1 cm | A.D. 1611 | Unchanged grazing and grasslands; unexplained hiatus around A.D. 1700 | Rather weak |
| MA-P7b | 83.7 cm | A.D. 1573 | Unchanged grazing on mire; grasslands came closer | Rather weak |
| MA-P7a | 85.1 cm | A.D. 1559 | Less grazing and no manuring on mire | Rather weak |
| MA-P6 | 86.65 cm | A.D. 1509 | Moderate grazing and manured grassland on mire | Moderate |
| MA-P5 | 88.0 cm | A.D. 1448 | Less grazing on mire; nutrient-poor heathland replaced the manured grassland | Rather weak |
| MA-P4b | 89.3 cm | A.D. 1323 | Strong grazing on mire; manured irrigated grassland was probably created on mire | Strong |
| MA-P4a | 89.9 cm | A.D. 1288 | Nearby heathland turning to grassland, probably hay meadow | Rather weak |
| MA-P3 | 90.9 cm | A.D. 1256 | Less grazing on mire; abandoned grassland nearby turning to heathland | Rather weak |
| MA-P2d | 91.5 cm | A.D. 1229 | Grazing on mire | Rather strong |
| MA-P2c | 92.1 cm | A.D. 1132 | Nearby deforestation; increased grazing near and on mire causing nutrient depletion; possible hiatus | Rather strong |
| MA-P2b | 92.7 cm | A.D. 1097 | Grazing on mire increased somewhat; some deforestation adjacent to mire | Moderate |
| MA-P2a | 94.7 cm | A.D. 1024 | Some regional burning and deforestation; some grazing on mire | Weak |
| MA-P1c | 95.1 cm | A.D. 1019 | Wetter mire, either through humans or naturally | Either strong or none |
| MA-P1b | 97.7 cm | A.D. 994 | Temporary expansion of <i>Pinus mugo</i> on the mire | None |
| MA-P1a | 100.5 cm | A.D. 974 | Anthropogenic grasslands present regionally | None |

Zone MA-P6 This zone has indications of human activity similar to Zone MA-P4b but less pronounced. The main differences are the lack of a Gramineae maximum and of a sediment accumulation minimum. We interpret it as a partial revival of the activities inferred for Zone MA-P4b.

Zone MA-P7a Indications of human activity become again less obvious, similar to Zone MA-P5. Recovery of the mire from more intense human impact would also explain the maximum in peat accumulation. The short-lived and marked maximum of both *Sphagnum* and *Tilletia sphagni* coincides with the partial replacement at the precise sampling spot of *Sphagnum fuscum* by *Sphagnum magellanicum* (Van der Knaap et al. 2011). This agrees with De Klerk et al. (2008), who quoted Hölzer and Hölzer's (1995) observation that *Sphagnum* sporulated mainly when one species succeeds another.

Zone MA-P7b The continuation of dung-related fungi suggests a continued low level of human impact on the mire. This, in combination with a minimum in peat accumulation and maxima of *Potentilla*-type, Compositae Subfam. Cichorioideae and *Calluna* reflects human activity at a closer distance than before.

Zone MA-P7c In view of a possible hiatus (see above), we ignore the minima present in accumulation rates (Fig. 3) but absent in percentages (Fig. 4). No change is evident neither in the dung-related fungi nor in grassland indicators after the ending of their maxima in the previous zone, so the mire might have been fairly undisturbed. The data do not provide any hint that might help to explain a hiatus or slowed peat accumulation, so it may have been caused by a chance event, such as an animal hoof damaging the moss layer.

Zone MA-P7d *Selaginella selaginoides* increased, first moderately and later (A.D. 1743) abruptly to a maximum, indicating that it grew on the very coring spot. Cyperaceae and *Potentilla*-type also increased. This may reflect the development of the hummock without any human impact.

Zone MA-P8 The temporal resolution in this zone becomes near-annual, and with it appear marked fluctuations in many pollen types (e.g., *Larix*, *Pinus cembra*, *Picea*). These fluctuations are so rapid that they cannot reflect plant-population dynamics and they are too pronounced to reflect statistical error, so we assume that they reflect fluctuations in pollen production and transport. Kamenik et al. (2009) explored the impact of weather conditions on this phenomenon for the period with measured climate data (A.D. 1864–2003), and found a strong relationship with pollen percentages, especially with

average April–November temperatures. This phenomenon is not further explored in this paper.

Zone MA-P8a The declines in dung-related fungal spores, *Potentilla*-type, *Ranunculus acris*-type and Gramineae indicate less grazing on the mire, and the maximum of *Andromeda* indicates a shift to more nutrient-poor conditions (bog). *Selaginella selaginoides* was declining but continued to be very abundant. The decline of *Calluna* and marked increase of Cyperaceae indicate wetter mire vegetation.

Zone MA-P8b *Selaginella selaginoides* nearly disappeared, Cyperaceae remained abundant, and *Caltha*-type re-appeared. A short-lived phase of abundant *Potentilla*-type started at 61.35 cm. Indications of human impact on the mire remain low, so the observed changes could represent shifting vegetation patterns independent of human activity. *Rumex obtusifolius*-type (group 7) became more frequent, which is a reflection of nutrient enrichment at the regional scale (Van der Knaap et al. 2000).

Zone MA-P9 The local mire vegetation changed; Cyperaceae declined, *Vaccinium* expanded, and *Sphagnum* (and *Tilletia sphagni*) suddenly started sporulating massively, this time without any shift in *Sphagnum* species. This indicates that the local *Sphagnum fuscum* hummock finally out-grew its surroundings, resulting in a drier surface. A further indication of a drier surface is the re-appearance of *Polytrichum strictum* macrofossils after their absence in zone MA-P8b reported by Van der Knaap et al. (2011). Short-lived maxima of *Potentilla*-type, *Andromeda*, *Empetrum*, *Vaccinium* and *Juniperus* indicate shifts of plant populations due to expansion of the hummock. The elevated microscopic charcoal in A.D. 1850–1880 is not matched by any palynological response. *Ligustrum* pollen (identified according to Punt et al. 1991) appeared after ca. A.D. 1610 and became more frequent after A.D. 1890, probably reflecting its planting in gardens regionally.

Extra-regional human impact

Group 8 in Fig. 4 includes the pollen types of plants sensitive to human impact at the extra-regional scale. *Castanea* and *Cannabis* both increased ca. A.D. 1030. These two and also *Olea* and *Ostrya*-type increased around A.D. 1588–1600, and *Castanea* increased additionally ca. A.D. 1117. *Cannabis* had two distinct declines, one around A.D. 1830/50 and then one around A.D. 1943. *Olea* shows a declining trend and *Ostrya* increasing after A.D. 1930. *Platanus hybridus* first appeared around A.D. 1850. Except for *Ostrya*, these trends probably follow cultivation practices. The timing of the *Cannabis* decline differs from that

in the northern Alps, where it occurred around A.D. 1900 (Van der Knaap et al. 2000). The *Ostrya* expansion reflects overgrowing of abandoned fields on the southern slopes of the Alps (Van der Knaap et al. 2000). The remarkable disappearance of *Pteridium* spores after about 1950 is a common feature in sites from the Alps and surroundings, and is as yet unexplained. *Castanea* (group 8) and the twelve pollen types of group 9 share a short period of distinctly lower values ca. A.D. 1850–1865. This may record the impact of Little Ice Age conditions on pollen production and/or transport.

Wengerkopf

The pollen types in the Wengerkopf diagram (Fig. 5) have been grouped according to growth form (trees, shrubs, herbs etc.), place in the landscape (altitude and presence/absence in the Lungau region today) and ecology (soil wetness, cultivated or not). The group of extra-regional trees and shrubs comprises taxa not growing in the region of Lungau today (Vierhapper 1935; Wittmann et al. 1987). Some of these are planted occasionally in villages on valley bottoms (e.g. *Quercus* and *Fagus*). Pollen analysis has shown that *Fagus sylvatica* did grow in Lungau in the past (Fritz 1967; Bortenschlager 1967; Krisai et al. 1991; Brosch 2000). The elevated *Fagus* pollen values during the early 17th century in the Wengerkopf diagram possibly reflect the last *Fagus* stands in Lungau. If we assume this for *Fagus*, it may also be assumed for *Quercus*, as the latter has a pollen curve in Wengerkopf very similar to that of *Fagus*, but this would need confirmation. The group of regional trees and shrubs comprises taxa growing today in Lungau but not near the study site. They grow in fragments of deciduous forest present in many mountain valleys along the lower edge of the spruce forest just above the grasslands of the valley bottom. Least frequent among these are *Acer* (*pseudoplatanus*), *Fraxinus* and *Ulmus*, which have their upper altitudinal limits not far above the valley bottom. Also *Abies* trees are infrequent, reported as occurring sporadically in the forest. Trees and shrubs growing today close to the coring site are grouped as (extra-) local trees and (extra-) local shrubs. Their pollen signal is not strictly local, as part of the pollen is probably derived from greater distances. Ericales that grow in the studied mire or other mires in Lungau are grouped as (extra-) local Ericales. Among these, the pollen signal of *Calluna* and *Vaccinium* is not strictly local, as they are also abundant outside mires. Herbs growing in mires are under the header ‘Wet’.

Trends in pollen types of the first two groups are essentially the same. Together they comprise about 15–40% of the pollen sum. This is an impressive

proportion for plant taxa not growing near the site, which may be related to the situation of the bog on the summit of a mountain, where pollen blows in from long distances.

Zone WEN-1 (start ca. A.D. 1595)

According to the pollen data, *Picea* and *Larix* dominated the forest in the surroundings of the site, *Alnus viridis* and *Betula* were abundant and may even have grown near the site, *Pinus cembra* was absent or very scarce on the mountain, and *Pinus mugo* s.s. (*Pinus* Subgen. *Pinus* pollen) did not yet grow on the bog (where it grows today). Cyperaceae, Gramineae, *Vaccinium*, *Calluna* and *Empetrum* were growing at or close to the coring location. Small amounts of pollen of many other grassland plants (*Rumex*, *Plantago* etc.) indicate that grasslands were not far away, so it is probable that the slopes of Wengerkopf were more heavily used for grazing and hay-making than is the case today. Low amounts of crop pollen indicate cultivated fields, but possibly situated at greater distances. During sub-zone WEN-1a, *Juniperus* (>6% pollen), Compositae Subfam. Cichorioideae and *Melampyrum* must have grown at the coring location. This indicates a dry bog surface, for which grazing by domestic animals could be responsible. It is tempting to interpret the *Picea* pollen maximum during sub-zone WEN-1b as a period of dense and shady spruce stand very close to the site, which temporarily suppressed the pollen production of *Juniperus* and *Alnus viridis* and favoured the growth of ferns (Monolete fern spores). The appreciable pollen percentages (>4%) of the light demanding *Larix* indicate that the inferred dense spruce stand must have covered a small area.

Zone WEN-2 (start ca. A.D. 1620)

Abruptly declining *Picea* pollen and gradually increasing *Juniperus* indicate increased openness of vegetation close to the site. The increase in microscopic charcoal and *Pteridium* suggests that fire played a role. Stable extra-regional pollen values indicate that the increased openness did not lead to more efficient pollen transport from longer distances, which supports the idea that only the direct surroundings of the site were opened. *Pinus cembra* increased, probably taking advantage of the local forest opening. In sub-zone WEN-2b, the slight *Picea* maximum and charcoal and *Pteridium* minima suggest spruce recovery and reduced fires. *Larix* also increased slowly, and *Juniperus* rather markedly. Pollen of the trees *Betula*, *Alnus incana*, *Corylus*, *Fagus* and *Quercus* declined gradually, but this is not matched by increased herb pollen. This mismatch suggests deforestation beyond the reach of appreciable herb-pollen transport, i.e. at larger distances.

Zone WEN-3 (start ca. A.D. 1700)

Indications of slightly increased local grazing, especially during sub-zone WEN-3a, are provided by *Urtica*, *Ranunculus acris*-type, *Lotus*-type, *Melampyrum*, *Selaginella selaginoides*, *Gentianella campestris*-type, dung-related fungi (*Cercophora*-type and *Podospora*), *Tilletia* (possibly suggesting nutrient enrichment) and gradually increasing Gramineae. *Picea* declined somewhat and both microscopic charcoal and *Pteridium* peak. The decline of most grazing indicators and marked maxima of *Juniperus*, *Carlina* and *Hypericum* in sub-zone WEN-3b indicate abandonment of pastures. A temporary recovery of *Alnus viridis* is probably related. Gradual declines of *Fagus* and *Quercus* in sub-zone WEN-3b represent either their final extinction in the region of Lungau or declines further away. *Ostrya* and *Fraxinus excelsior* increased modestly at the same time. The appearance of *Cerinth* is remarkable. This rarely encountered pollen type has low productivity and dispersal capabilities, and the species *Cerinth minor* is very rare in the region today. It most probably grew close to the site in open grassland on the south-exposed slope just below the mire (where there is open forest today). In sub-zone WEN-3c, *Picea* increased and charcoal declined. Again, *Pteridium* followed the charcoal trend. Also grassland indicators Gramineae and *Juniperus* declined.

Zone WEN-4 (start ca. A.D. 1850)

This zone marks a rather abrupt change in vegetation taking place in one or two decades. The trees growing close to the site (*Picea*, *Pinus cembra* and *Pinus mugo* s.s.) expanded, overshadowing *Juniperus* so that the latter produced less pollen, and Gramineae declined. At the same time fire activity declined (less microscopic charcoal and *Pteridium*). The appearance of *Blechnum* and *Oxalis* is probably related to the soil acidification caused by conifer litter. These changes probably represent reforestation of the abandoned pastures close to the site. Other grassland plants (*Plantago lanceolata*, *Rumex acetosa*, *Urtica* etc., and dung-related fungal spores) did not decline, indicating that grazing did not stop completely. Hay meadows may also have existed; some were known to exist and were annually mown up to about A.D. 1960 near Dürrenecksee and at Wenger Alm, situated a few hundred metres from the site (pers. comm. Peter Lintschinger, Tamsweg). Pollen of some cultivated and introduced plants at lower elevation appeared during the course of the zone: *Platanus*, *Ligustrum*, *Amaranthus* and *Ambrosia*. Sub-zone WEN-4b marks the transition from fen peat to *Sphagnum* hummock. As a result, the temporal resolution becomes near-annual, and with it appear marked fluctuations in many pollen

types (e.g. *Picea*), as was found at Mauntschas, zone MA-P8. The hummock became a miniature ungrazed patch surrounded by pasture. Pasture is confirmed by the continuation of most grassland plants, and hummock formation by the decline of low-growing grassland plants that have such extremely limited dispersal capacities that only few of their pollen and spores made it to the top of the hummock (dung-related fungal spores, *Campanula*, *Trifolium repens*-type and *Trifolium pratense*-type).

Zone WEN-5 (start A.D. 1950)

In sub-zone WEN-5a, *Picea* increased massively, overshadowing *Juniperus* close to the site so that the latter produced much less pollen. *Cannabis* and *Secale*, growing at lower elevation, declined markedly. Vierhapper (1935) mentions the cultivation of *Cannabis* in the region, but this had stopped after World War II. Microscopic charcoal declined further and *Pteridium* spores disappeared from the record, which indicates effective fire suppression in the region. Nevertheless, *Pteridium* plants have not disappeared from the landscape, not even from the Wengerkopf mountain. This confirms the observation that *Pteridium* can sporulate abundantly after fire (Conway 1957). In sub-zone WEN-5b, *Pinus mugo* s.s. expanded on the edge of the bog where it is still abundant today; this further suppressed *Juniperus*. This local change in vegetation seems to have little affected the grassland plants, so we interpret it as a shift in vegetation patterns close to the site. The *Sporormiella* maximum indicates an animal dropping on the bog very close to the hummock. Several extra-regional and regional deciduous trees increased (*Ostrya*, *Quercus*, *Alnus glutinosa*, *Alnus incana*, *Betula* and *Corylus*), which can be explained by (partial) abandonment of marginal pasture. *Cannabis* and *Secale* cultivation declined further, and *Ambrosia* increased. In sub-zone WEN-5c *Ostrya*, *Alnus glutinosa*, *Alnus incana* and *Betula* continued to increase, and *Fagus* and *Fraxinus excelsior* also increased. *Corylus* did not increase any further, suggesting that its gain in cover area as a pioneer shrub on abandoned pasture was balanced by its loss through succession to taller forest. *Bellis* appeared.

Rosaninsee

The pollen diagram for Rosaninsee represents less than half a century and the temporal resolution is approximately annual (Fig. 6). The rapid fluctuations in many pollen types reflect therefore fluctuations in pollen production rather than population dynamics. The location is open and wind-exposed, so that all tree pollen is of regional or extra-regional origin, with the possible exception of *Alnus viridis* and *Pinus* Subgen. *Pinus* (*Pinus mugo* s.s.).

Zone ROS-1

In this zone *Alnus viridis* and ferns (Monolete fern spores) were probably growing close to the site, where they are absent or rare today.

Zone ROS-2

Here *Alnus viridis* declined gradually. Conifer trees increased (*Picea*, *Pinus cembra*, *Pinus mugo* s.s.), which probably reflects the abandonment of marginal pasture in the region. A phase of elevated *Potentilla* follows directly after a single-spectrum maximum of the dung-related fungus *Podospora*-type, which suggests that local dung deposition favoured *Potentilla* expansion or flowering. In sub-zone ROS-2b, *Cannabis* cultivation at lower elevation declined. Indicators for local grazing and several grassland plants had maxima (dung-related fungal spores, *Selaginella selaginoides*) or continued to have elevated values. In sub-zone ROS-2c, *Cannabis* declined further, *Ostrya* increased, and grazing pressure eased locally.

Zone ROS-3

Gramineae declined in the local vegetation. This may be the result of acidification due to peat formation on ombrotrophic hummocks, one of which is the sampled hummock. In sub-zone ROS-3b, indicators for local grazing (*Sporormiella*) and several grassland taxa had short-lived maxima (*Campanula*, *Potentilla*-type, *Ranunculus acris*-type), which suggests increased nutrients. In sub-zone ROS-3d, *Pinus mugo* s.s. (*Pinus* Subgen. *Pinus* pollen) expanded in the surroundings.

Regional pollen trends

In an earlier study, trends in a number of regional pollen types appeared to be consistent for the entire western Swiss Alps (Van der Knaap et al. 2000). This holds in part for the new sites. Twentieth century pollen/spore trends that are similar to earlier results include the appearance and later increase of *Ambrosia*, the increase of *Ostrya*-type, *Fraxinus excelsior* and *Fraxinus ornus*, and, at Mauntschas and Wengerkopf, the disappearance of *Pteridium aquilinum* after A.D. 1950. *Mercurialis annua* was found to decline after A.D. 1950 in the earlier results, whereas at Wengerkopf it did not decline.

In an earlier study, trends in *Cannabis* pollen were found to be synchronous in the western Swiss Alps and Jura Mountains during the last millennium (Van der Knaap et al. 2000), so with caution they can be used to synchronize pollen diagrams. It is therefore worth looking at whether *Cannabis* trends are synchronous in a larger area.

In the pollen diagrams of this study, the *Cannabis* curve has vaguely similar shapes with one or several early increases and late declines. However the timings differ in part, which can either be real or due to deviation of depth-age models from the real depth–age relationship. As discussed above, the depth–age model is considered to be good for Mauntschas, good for Wengerkopf after A.D. 1950 and rather good before it, and basically correct for Gouillé Rion (though with a large uncertainty). The points of similarity among diagrams include the following: (1) *Cannabis* is at its minimum at the top of the diagrams. (2) The last *Cannabis* decline just prior to the mid-20th century agrees well between Mauntschas, Gouillé Rion and Wengerkopf and with earlier studies. Its slightly earlier date (A.D. 1930) at Gouillé Rion compared to the other sites (A.D. 1945) might be real or the result of dating uncertainty. (3) An early-19th-century *Cannabis* decline agrees well across the three mire sites. (4) The *Cannabis* increase, dated A.D. 1590 at Mauntschas, might be synchronous with the one dated A.D. 1620 at Wengerkopf. (5) The ill-defined *Cannabis* maximum dated around A.D. 1800, both at Mauntschas and Wengerkopf, might represent the same event. (6) The *Cannabis* increase dated A.D. 1030 at Mauntschas is possibly the same as the one dated A.D. 850 at Gouillé Rion, if we accept an uncertainty of nearly 200 years in the latter. A difference between sites also occurs: *Cannabis* increased around A.D. 1430 at Mauntschas but declined at Gouillé Rion. The events are approximately synchronous even when large dating uncertainties are assumed, and therefore suggest a difference in the *Cannabis* cultivation history between the pollen-source areas of the two sites.

Discussion

Effect of high temporal resolution on pollen signal

The near-annual to sub-decadal temporal resolution applied brings two phenomena to light that were previously little regarded in palaeoecology. One is flowering cycles (low and high flowering years) of plants, especially trees, which have been shown to depend at least in part on weather fluctuations (Van der Knaap and Van Leeuwen 2003; Kamenik et al. 2009). Also Beug (2011) found flowering cycles of several tree species in a pollen diagram from northern Germany with a temporal resolution of 3–5 years. The other phenomenon is the occasional mass transport of pollen or spores by agents other than wind. At Wengerkopf (Fig. 5), for example, several otherwise infrequent pollen and spore types have mass occurrences in single samples – some very pronounced, e.g. *Achillea*-type 353 grains at 51.5 cm, *Ranunculus acris*-type 110 at 58.5 cm and

Dryopteris filix-mas-type 80 at 60.75 cm; others less so, e.g. *Hypericum perforatum*-type 20 at 35.0 cm and *Solidago* 12 at 69.2 cm. We interpret this as either inclusion of anthers, flowers, or sporangia in the pollen samples or as pollen transport by animals. The peaks have therefore a fundamentally different relation to plant abundance than the values of regular wind-dispersed grains, so the resulting minima in tree-pollen percentages have no significance in terms of plant abundance. The *Hypericum* peak at 35 cm at Wengerkopf coincides with peaks of the dung-related fungus *Sporormiella*, *Tilletia sphagni* and the tree *Castanea* (35 grains); the latter does not grow in the region of Lungau and has its closest stands in Carinthia, about 80 km to the south. This indicates that the sample may include dung from animals foddered on material containing *Castanea* pollen, which implies distant transport of the fodder. We double-checked the identification of *Hypericum* and *Castanea* pollen because the morphological separation can be difficult (see discussion in Krebs et al. 2004), especially when *Hypericum* pollen is in part not fully ripe, as is probable when the plants were consumed by cattle. Two peaks of *Fagus* pollen at Wengerkopf (24 grains at 47.8 cm, 26 at 16.25 cm) are difficult to interpret, because these trees were absent from the region of Lungau in those times (after A.D. 1940), which implies that the pollen must have travelled far, crossing high mountains. Inclusion of flowers, anthers, or pollen-bearing insects will result in less pronounced peaks when the peat is sampled at lower temporal resolution. A suspected case—among many—is *Rhododendron*, with 10 grains at 67.2 cm at Wengerkopf. At much lower temporal resolution, short-lived pollen peaks may be smoothed to the degree of passing unrecognized, and then this pollen may be interpreted in terms of past plant abundance. At intermediate temporal resolution the significance of pollen peaks may be a matter of speculation. The use of pollen accumulation rates is helpful as it prevents the percentage effect on other pollen types (e.g. Fig. 3). In earlier high-resolution studies of mires we also found short-lived herb pollen peaks (e.g. Praz Rodet in the Swiss Jura Mountains, Älbi Flue and Aletschwald in the northern and central Swiss Alps, respectively. Van der Knaap et al. 2000; Van der Knaap and Van Leeuwen 2003). In most cases peaks of dung-related fungal spores accompanied the herb-pollen peaks, so pollen transport in dung was the obvious explanation.

Depth-age modelling and PAR

Goslar et al. (2009) described the development of the chronology for Mauntschas mire studied here, using ‘free-shape age–depth modelling’. In this approach, three conditions need to be fulfilled for the best fit of the depth–age model to the data, namely the fit of the ^{14}C dates to the

radiocarbon calibration curve, a high smoothness (no abrupt changes) of the depth–age line, and a high smoothness of PAR (pollen-accumulation rates or influx; grains $\text{cm}^{-2} \text{year}^{-1}$) of the sum of dominant regional pollen types. The algorithm of ‘free-shape age–depth modelling’ searches for a reasonable equilibrium or compromise between the three conditions. Below we consider the implications for palaeoecological interpretation of these criteria on the example of Mauntschas.

The construction of any accurate chronology before A.D. 1950 is confronted with the basic problem that the confidence intervals of sample ages judged solely from AMS radiocarbon dates are mostly large (up to several decades) compared to the (modelled) intervals between sample midpoints (often below 10 years). Radiocarbon dating alone allows an almost endless range of depth–age curve shapes within the limits of the confidence intervals, varying from relatively stiff curves to more wiggly variants. For Mauntschas, stiffer, less flexible variants resulted in conspicuous fluctuations in PAR that are very similar amongst the majority of dominant ‘regional’ pollen types (i.e. types included in the pollen sum used for percentages), whereas a wiggly variant could be created that resulted in fluctuations in PAR that are more independent among the dominant regional pollen types. Stiffer depth–age models are based on the null-hypothesis that peat accumulation rates do not fluctuate rapidly, which is partly falsified by radiocarbon dating. Wiggly depth–age models are based on the null-hypothesis that the PAR of the sum of dominant regional types does not fluctuate rapidly, which is then partly falsified by the radiocarbon dating. The smoothest PAR curve possible within the limits set by radiocarbon dating would result in a very wiggly depth–age curve. In fact, this would bring the trends in calculated PAR as close as possible to trends in pollen-percentages within the limits set by the radiocarbon dating. The final depth–age model used both null-hypotheses in the form of conditions: average PAR of dominant regional pollen types should not show abrupt changes over short vertical distances (time spans) in the peat section, and the peat accumulation rate should not change strongly over short vertical distances. It uses as the third condition a good fit of the ages of radiocarbon-dated levels to their calibration curves. The question arises whether the null-hypothesis of no abrupt changes in average PAR is a reasonable assumption. It may not be so; the true (but unknown) PAR might show rapid shifts due to abrupt vegetation change or to abrupt climate change. We tried to exclude abrupt vegetation change by selecting only abundant regional pollen types for the depth–age modelling, all representing large plant populations growing mostly at a larger distance from the study site, and not showing abrupt shifts in their pollen percentages. It is reasonable to assume that the regional vegetation (as

reflected by these pollen types) did not undergo rapid changes when the pollen percentages do not indicate any. Abrupt climate change, on the other hand, might potentially cause PARs of all pollen types to shift simultaneously in the same direction, in disagreement with the null-hypothesis. A marked cooling, for example, simultaneously suppresses the pollen production of at least several of the dominant regional types. This possibility must be taken seriously, but can only be accepted when hard data show it. The null-hypothesis must therefore be ‘no abrupt shifts in PAR’, and at Mauntschas the hard data of radiocarbon dating failed to reject it. We may therefore have missed a climate-induced signal in the true-but-unknown PAR, but there seems no possibility to extract it from this dataset. A potential problem is that the criterion of ‘no abrupt shifts in PAR’ results in large shifts in peat accumulation rates, thus counteracting the criterion of ‘no abrupt fluctuations in peat accumulation rates’ of the other null-hypothesis. We have, however, seen that the microfossil record from Mauntschas provides support for the most marked shifts in peat accumulation rate and for some of the lesser shifts. This justifies giving less weight to the latter criterion.

Alpine mires modified by human impact

Most human impact recorded in the peat sections (Mauntschas, Wengerkopf and Rosaninsee) concerns cattle grazing and related events such as modified mire hydrology and burning. We found indications for (a) the former presence of cattle (dung-related fungal spores), (b) surface damage by cattle (peat accumulation rates), (c) nutrient enrichment of the mire vegetation (pollen), (d) modified hydrology assumed to be deliberate (pollen), (e) small-scale deforestation and small-scale burning close to the mire (charcoal, pollen) and (f) pasturing outside the mire (pollen). Active grazing still takes place at Wengerkopf and Rosaninsee, whereas Mauntschas has been protected from grazing for some centuries. The pollen/spore signal of Mauntschas during this period, however, does not show the local absence of cattle so clearly. It includes (1) scattered dung-related fungal spores and (2) plenty of pasture-related herb pollen. This can be explained by field observations that (1) grazed fields as the source of the fungi are only a few hundred metres away, and (2) pasture-related herbs still grow along the mire edges and in the immediate surroundings, especially along the numerous tracks. So, even after centuries, the mire and the landscape have not fully recovered from the earlier human impact.

In Sjögren et al. (2007) we discussed the difficulty of finding any pristine mire in the Jura Mts or the European Alps. Nine mires were studied, including Wengerkopf and Rosaninsee, but not Mauntschas. All the nine mires had a peat stratigraphy which included a decomposed peat layer

below the well-preserved upper *Sphagnum* peat. We interpreted the decomposed layer as resulting from grazing and trampling by domestic animals one to three centuries ago. Mauntschas, on the other hand, was the only mire we could find in the Alps that does not show this peat stratigraphy, at least locally. We therefore imagined finally having found a pristine mire, or at least the ideal peat section where climate would dominate the biological proxies rather than human impact. In the multi-proxy study of the Mauntschas peat section, however, we showed that human impact dominates the pollen signal (Van der Knaap et al. 2011). Notable human impact on the mire ended about five centuries ago, and the local mire vegetation is still in the process of recovery.

Common pollen trends

A number of pollen types were shown to have trends that are similar, though not identical, among sites hundreds of kilometres apart. *Cannabis* is one of these. In general, trends during the 20th century show close agreement among the study sites, whereas trends during earlier centuries show more variation. Several causes may contribute to the increase of agreement towards the present: (1) Land-use practices became increasingly globalized, which gradually suppressed regional differences. (2) Most of the relevant pollen diagrams are more detailed towards the present, increasing the chance of detecting trends in rare types, such as *Mercurialis annua*. (3) The pollen diagrams have better age control towards the present due to post-bomb radiocarbon dating and ^{210}Pb dating, increasing the possibility of correctly synchronizing pollen trends.

Summary and conclusions

Three mires and a small lake in the Swiss and Austrian Alps were investigated for pollen at high temporal and pollen-morphological resolution, covering the last thousand years or less. In the mires, the pursuit of high temporal resolution and pollen influx has led to various methodological insights and considerations:

- (i) Amazingly high temporal resolution can be reached in peat deposits. Almost undecomposed *Sphagnum* peat can be sub-sampled at near-annual resolution, whereas more decomposed peat can be successfully sub-sampled at 0.2 cm intervals. In our peat sections from the Alps, sub-sampling the decomposed sections at 1 cm intervals would not have been sufficiently close to catch even the major phases of human impact.
- (ii) Pollen transported in clumps by animals or wind result in single-spectrum maxima that are higher

when the temporal resolution is higher. Such maxima do not reflect vegetation in the way that individually-dispersed pollen grains do, and if the pollen type is part of the pollen sum, the associated minima in other pollen types do not reflect vegetation dynamics. The latter problem does not exist when PAR (pollen influx) is used.

- (iii) Ideally, pollen curves in diagrams should directly reflect vegetation dynamics. PAR is often thought to give the best reflection. The calculation of PAR, however, is sensitive to even minor errors in the depth–age model related to sedimentary or peat-growth processes. Percentages are more robust, even though the interpretation in terms of plant abundance is hampered by percentage effects. A comparison of PAR with percentages is therefore always useful and recommended.
- (iv) In the algorithm of free-shape depth-age modelling, modelling on the basis of dated levels is extended by trying to avoid abrupt shifts in PAR and in sediment accumulation rates (Goslar et al. 2009). These criteria can be weighted independently and locally in the modelling. The criterion of avoiding abrupt shifts in PAR should be given extra weight when such shifts are important for the interpretation, for example in terms of climate change.

The pollen diagrams yielded a wealth of detailed results in terms of past human impact on vegetation. In summary:

- (a) In spite of extensive search, we did not find any mire in the Alps that remained undisturbed by humans during the entire last millennium. Mauntschas mire in the south-eastern Swiss Alps comes nearest, as it had relatively little human impact during the last five centuries.
- (b) In the results presented here, trends in pollen types reflecting regional human action are in good agreement with earlier findings for the western Swiss Alps (Van der Knaap et al. 2000), allowing for regional differences.
- (c) The small lake Gouillé Rion, situated just below the potential tree limit in the central Swiss Alps, was surrounded by pasture since A.D. 800. It records forest dynamics at lower elevations and an erosional phase in the catchment during the Little Ice Age.
- (d) Mauntschas mire, situated in the upper conifer belt of the south-eastern Swiss Alps, was periodically used for grazing and hay-making between A.D. 1000 and about 1550. After that, the local mire vegetation regenerated and ombrotrophic hummocks formed. Today, the vegetation of the mire, and especially of its close surroundings, still shows traces of the former human impact.
- (e) Wengerkopf mire, situated in the upper conifer belt of the central Austrian Alps, records vegetation change since ca. A.D. 1600. Regional land-use intensified gradually, and the complete extinction of *Fagus* and *Quercus* during the 17th century is recorded. The mire was grazed continuously, with maximum intensity during the 19th century. It became partly overgrown with trees during the mid-20th century.
- (f) Rosaninsee mire, situated at the tree limit in the central Austrian Alps, covers the second half of the 20th century. A moderate increase in forest-limit conifers indicates some decline of grazing. Regional pollen trends are very similar to those at Wengerkopf.

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